EFFECTS OF ANTHROPOGENIC NOISE ON ANTIPREDATOR REACTIONS AND BOLDNESS IN A FRESHWATER FISH

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in Partial Fulfillment of the Requirements
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By
Md Robiul Hasan

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Abstract

Anthropogenic noise pollution is increasing on a global scale, yet research aimed at understanding the potential impacts of anthropogenic noise is lacking. Detrimental effects of anthropogenic noise on marine species include altering hearing sensitivity, foraging, navigation, communication, boldness, and even risk perception. In freshwater systems, little is known regarding how anthropogenic noise impacts antipredator behaviour and boldness of prey fishes. To investigate such potential impacts, I exposed fathead minnows, *Pimephales promelas* to a playback of field recorded motorboat noise while exposing them to chemical alarm cue – an indicator of predation risk. I found that the boat noise exposure led to impaired antipredator responses to risk cues. I then examined effects of chronic lab-based noise on boldness in fathead minnows. I exposed minnows to either a familiar airstone noise or a novel filter noise for 8 days and then measured the latency of minnows to emerge from an isolation chamber as a standard measure of boldness. I found that minnows decreased their boldness with exposure to the novel acoustic environment. Surprisingly, I found no evidence for acclimation to the novel noise over the 8-d period. I also found that minnows recovered from the stress of the novel acoustic environment sooner when they were transferred to their familiar noise environment. My data suggest that aquatic species are negatively affected by anthropogenic noise both in their natural habitat and in the laboratory. My data indicate that management plans should consider taking action to mitigate noise pollution.

Acknowledgements

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Format of the Thesis

This thesis has been prepared as a manuscript-style thesis.

Chapter 1: General Introduction

1.1 General information

Natural habitats, including aquatic habitats, have been altered by human activities in many ways. Indeed, industrialization and climate change are prime threats to aquatic ecosystem globally (Crain et al., 2009; Halpern et al., 2007; Vörösmarty et al., 2010). Since anthropogenic activities are not slowing, it is necessary to understand how their impacts are detrimental to wildlife. Researchers have already made a lot of progress in fully understanding the adverse effects of many anthropogenic stressors. However, many more are still understudied. One such stressor, is anthropogenic noise, which has recently received increasing attention for its possible impacts on the underwater world (Cox et al., 2016).

Sounds that can interfere with the regular activity of animals or humans is considered noise. Noise is now likely a much more widespread pollutant in both aquatic and terrestrial environment than at any point in history (Shannon et al., 2016). In aquatic environments, sound can be generated by recreational activities such as power boating and whale-watching boats, ferries, commercial ships, energy exploration (e.g., seismic surveys), construction (e.g., pile driving), fishing, and naval sonar (Shannon et al., 2016; Whitfield and Becker, 2014). On land, however, sources are slightly different, and include urban development, resource extraction, as well as aircraft and automobile traffic (Barber et al., 2010; Blickley and Patricelli, 2010). Consequently, anthropogenic noise pollution has become a significant threat to wild animals, resulting in alteration of biological responses (Barber et al., 2010; Slabbekoorn et al., 2010). The presence of noise can alter an animals physiology, mating behaviour, foraging behaviour, movement, settlement behaviour, vocalization, and antipredator behaviour (Shannon et al., 2016). As wildlife is being severely affected by noise, we need a clear understanding of the detrimental effects to mitigation impacts.

1.2 Known effects of anthropogenic noise

Anthropogenic noise is known to affect terrestrial and aquatic animals. In terrestrial environments, aircraft and road traffic noise may cause hypertension in humans which is directly linked to heart disease and stroke (Jarup et al., 2008). Noise studies on humans are relatively sparse in the literature, most studies focus more on birds. In addition, reptiles and frogs are also known to be affected by noise. In birds, vocal signals (i.e., song) are well-studied aspects of the acoustic world. Such signals are used in a variety of contexts, including courtship, nesting and alarm calls. The Great tit, *Parus major,* shows altered courtship due to the difference in song frequency and intensity, resulting from urban noise (Salaberria and Gil, 2010). Polak et al., (2013) found that the breeding community of woodland birds reduced their nesting near noisy road ways. Exposure to traffic noise results in smaller clutches and a decreased number of fledgings from female great tits (Halfwerk et al., 2011). In addition, exposure to loud sounds may cause physical damage to bird's ears. Niemiec et al., (1994) demonstrated that four hours of exposure to octave-band noise (116 dB) causes hearing loss in quail, *Coturnix coturnix*. However, animals exhibit a complete recovery of hearing loss at five weeks post-exposure to sound. Similarly, hearing loss is also found in other birds such as canaries, *Serinus canaria*, and zebra finches, *Taeniopygia guttate* (Dooling and Popper, 2007). Such hearing loss is significantly correlated with cognitive and behavioural functions (Arlinger, 2003). Great tits fail to produce or perceive conspecific alarm call when they are exposed to noise, resulting in increased predation (Templeton et al., 2016). In another study, great tits reduced their foraging and failed to produce alarm calls in exposure to the peak of aircraft noise (Klett-Mingo et al., 2016). Reduced foraging due to noise is also found in other birds such as chaffinches, *Fringilla coelebs*, and owls (L. Quinn et al., 2006; Senzaki et al., 2016). Therefore, reproduction, behaviour, and community structure of birds are likely to be impacted from the negative impacts of noise pollution.

Although anthropogenic noise can negatively affect animals in terrestrial environments, it is likely to have much more significant effects on animals in aquatic ecosystems due to the physics of sound transmission. Sound travels very efficiently through water compared to air because of the high molecular weight of water. The velocity of sound in water is approximately five times faster than in air. This means that a specific wavelength of noise is likely to travel five times farther in water than in air (e.g., for 150 Hz signal: 4 m in the air, 20 m in water)

(Slabbekoorn et al., 2010). The underwater noise produced by ships, motorboats and other anthropogenic activities can, therefore, be detected much farther away from the source. Since sound travels farther in water, the aquatic environment is likely to be noisier as a result of increasing anthropogenic activities. Such noise can have detrimental effects on communication, physiology, reproduction, and behaviour of fishes and other aquatic animals.

1.2.1 Effects of noise on communication and physiology

Underwater sounds act as a medium through which many aquatic animals (e.g., sciaenids, oyster toadfish, marine mammals, and fishes) communicate (Mann, 2016; Richardson et al., 1998). However, chronic or acute anthropogenic noise can inhibit the perception of natural sound (Barber et al., 2010; Codarin et al., 2009). Consequently, the ability of fishes to hear natural sound may interfere in two ways. One way is the masking of communication cues – that is high-intensity sound overlaps the low-frequency hearing range of fish and subsequently affects communication and other behaviours (Slabbekoorn et al., 2010). In another way, high sound pressure levels can damage the inner ear sensory cells and cause hearing loss in fishes (Smith, 2016). Fishes have an air bladder, lateral line, and two inner ears inside the cranial cavity, which are used for hearing. The structure of the inner ear found in fishes is similar to that of all other vertebrates (Ladich and Popper, 2004). Sounds are converted into neural signals through specialized mechanosensory receptors called sensory hair cells (Coffin et al., 2004). High-intensity sounds cause damage to the sensory hair cells, resulting in temporary or permanent hearing loss. The goldfish, *Carrasius auratus,* exhibits significant sensory hair cell damage and hearing loss when exposed to noise stimulus at 170 dB re 1 μPa (or 124 dB re 1 μPa) (Smith et al., 2004). Similarly, the pink snapper, *Pagrus auratus,* exhibits sensory hair loss and hearing loss when exposed to air-gun noise (McCauley et al., 2003). However, hearing recovery may also happen in fishes within two or three weeks after the loss of hearing. The goldfish took more than 15 days, and the fathead minnows took 14 days to return to a normal state of hearing (Scholik and Yan, 2001; Smith et al., 2006).

Besides hearing loss, human-induced noise can also elicit physiological stress responses in animals (Popper et al., 2003). Goldfish exhibited an increase in plasma cortisol level after 10

minutes of exposure to 170 dB noise (Smith et al., 2004). Blacktail shiners, *Cyprinella venusta*, also had increased cortisol levels after acute exposure to road traffic noise (Crovo et al., 2015). Similarly, three freshwater fishes: common carp, *Cyprinus carpio*, gudgeon, *Gobio gobio* and perch, *Perca fluviatilis*, exhibit elevated plasma cortisol when exposed to the playback of ship noise at 153 dB (Wysocki et al., 2006). Moreover, ventilation (opercular beat rate) and active metabolic rate (oxygen usage) of fish has been documented as indicators of physiological stress response induced by noise (Barton, 2002). Elevation in metabolic rates are found in several species when exposed to ship or motorboat noise (Simpson et al., 2016, 2015; Wale et al., 2013). Such species include crab, *Carcinus maenas*; eel, *Anguilla anguilla*; and ambon damselfish, *Pomacentrus amboinensis.* In addition, increased heart rate and decreased swimming stroke rate has been observed in largemouth bass, *Micropterus salmoides,* in the presence of boat disturbance (Graham and Cooke, 2008a). Such physiological stresses induced by anthropogenic noise can have behavioural consequences in aquatic animals (Popper et al., 2003). Therefore, essential aspects of life such as reproduction and other vital behaviours are likely to be affected by anthropogenic noise.

1.2.2 Effects of noise on reproduction

Acoustic signals represent a well-known feature for courtship in many fish species (Amorim et al., 2003; Lobel, 1992; Lobel and Mann, 1995; Lugli et al., 1995). Such species include tilapia, *Oreochromis mossambicus*; damselfish, *Dascyllus albisella*; common goby, *Padogobius martensii* and panzarolo goby, *Knipowitschia punctatissima*; hamlet, *Hypoplectrus unicolor* (Serranidae) and striped parrotfish, *Scarus iserti* (Scaridae). Since reduced perception of acoustic signals results from anthropogenic noise, it appears to be detrimental to courtship, hatching of fertilized eggs, larval development, and growth of individuals (Slabbekoorn et al., 2010). However, direct studies examining courtship of fish under acoustic disturbance are rare. One recent study found that the intense noise exposure resulted in reduced courtship in the female painted goby, *Pomatoschistus pictus*, during spawning (de Jong et al., 2017). Although few studies assessed hatching, larval development and growth of fishes, none of them showed significant adverse effects of chronic or acute noise. Four weeks exposure to playback of boat noise had no significant effects on hatching success, larval growth, and survival of the cichlid

fish, *Neolamprologus pulcher* compared to fish in the control treatment (Bruintjes and Radford, 2014). Similarly, growth and survival of rainbow trout, *Oncorhynchus mykiss,* were not affected by the chronic exposure to noise (Davidson et al., 2009; Wysocki et al., 2007). In contrast, embryonic development of some marine invertebrates have been impaired because of background noise pollution. For example, noise causes delayed embryonic development (21%) and increased mortality of newly hatched larvae (22%) of the sea hare, *Stylocheilus striatus* (Nedelec et al., 2014). Similarly, a delay in larval development and high rates of larval deformities (46%) occurred in scallops exposed to seismic pulses (De Soto et al., 2013). Also, the brown shrimp, *Crangon crangon* exhibited reduced growth and reproduction in exposure to elevated noise levels compared to those exposed to ambient noise control (Lagardère, 1982). Therefore, noise pollution could be a significant factor for reproductive dysfunction.

1.2.3 Effects of noise on behaviour

There is growing evidence that anthropogenic noise has the potential to affect the behaviour of aquatic animals. Although not all species are equally susceptible to noise, recent studies have given us the opportunity to address the severity of noise pollution on diverse types of behaviour in fishes, aquatic mammals, and other invertebrates. Blue whales, *Balaenoptera musculus,* emit fewer calls when experiencing SONAR, whereas the call production is increased in the presence of ship noise (Melcón et al., 2012). Such vocalization is likely linked with social interaction within the whale population (Oleson et al., 2007). In cooperatively breeding cichlid fish, *Neolamprologus pulcher*, social interactions also shifted in the presence of boat noise (Bruintjes and Radford, 2013). As such, dominant males had lower nest digging frequency when exposed to a playback of boat noise compared to the ambient noise control, however, in case of dominant females, there was no significant difference regarding nest digging frequency between treatments. Such alteration in social behaviours can have negative consequences in community ecology.

In addition, food acquisition by individuals is also likely to be affected by anthropogenic noise, as seen in the Mediterranean coastal damselfish, *Chromis chromis,* who frequently experience recreational boat noise during the day. Interestingly, damselfish show

lower feeding frequency, particularly when boat traffic is more significant (Bracciali et al., 2012). Magnhagen et al., (2017) found that the roach, *Rutilus rutilus*, and perch, *Perca fluviatilis* had fewer feeding attempts when exposed to boat noise compared to controls. Moreover, ship noise is also known to reduce foraging success of humpback whale, *Megaptera novaeangliae*.

Animal boldness is another crucial behaviour which can also be affected by anthropogenic noise. Boldness and shyness are often considered as general personality traits that are expressed in different situations (Stamps and Groothuis, 2010). The terms 'bold' and 'shy' refer to the propensity of an individual to take risks, but this personality trait is not necessarily synonymous with fearful behaviour (Sih et al., 2004). The bold-shy continua found in every group of animals including fishes, mammals, birds, amphibians, and invertebrates (Conrad et al., 2011). Consequently, this trait is known to affect survival and reproduction, the tendencies of an individual being caught by fishing nets, exploitation of food and predator encounter rate (Ballew et al., 2017; Biro and Dingemanse, 2013; Sih et al., 2004; Stamps, 2007). One recent study found that the damselfish, *P. amboinensis* exhibit reduction in boldness when exposed to the playback of motorboat noise for a brief time (Holmes et al., 2017). From that study, it assumed that the sound might not be novel to fish as they are wild caught. Therefore, further investigation is necessary to determine whether, and how, novel sound affects the boldness behaviour in fishes.

Besides boldness, predator-prey interactions are a universal phenomenon in community ecology. Since noise causes auditory damage and hearing loss, prey could not recognize their predators and communicate with their conspecific for a short period (Popper et al., 2003). As a result, predation related mortality could happen. Salmonid smolts, *Oncorhynchus tshawytscha* show higher mortality due to predation when they are close to hydroelectric dam passage, but such mortality to predation is not found in salmonids that are not close to the dam passage (Mesa, 1994). Few recent studies found that anthropogenic noise such as ship or motorboat noise can have detrimental effects on prey behaviour in the presence of simulated or live predator attacks (Simpson et al., 2016, 2015; Voellmy et al., 2014). For example, in the presence of a simulated predator attack, the European eel, *Anguilla anguilla* is 50% less likely to exhibit a startle response while experiencing background ship noises compared to the controls (Simpson et al., 2015). Subsequently, another study found that ambon damselfish, *Pomacentrus amboinensis*

suffer increased mortality associated with predation when motorboat noise pollution occurs (Simpson et al., 2016). So, it is clear that boat noise can impair antipredator behaviour of prey in the presence of a simulated or live predator, but the underlying mechanism for how prey behaviour is affected remains unclear. In a study on hermit crabs, *Coenobita clypeatus*, individuals were exposed to anthropogenic noise and displayed slower reactions to visual cues of an approaching predator. The authors proposed the 'distracted prey hypothesis' to account for these results, arguing that processing noise interferes with processing other information in the brain (Chan et al. 2010).

1.2.3.1 Alarm cue mediated antipredator behaviour

Damage released chemical alarm cues are released into the environment when a nearby conspecific is injured or killed during a predator encounter (Chivers and Smith, 1998). These chemicals are located in the epidermis of teleost fish and other aquatic animals and represent a potentially high level of predation risk for prey species able to detect them (Chivers and Smith, 1998). Chemical alarm cues found in a variety of aquatic organisms, including gastropods, damselflies, amphipods, amphibians, and fishes (Appleton and Palmer, 1988; Chivers et al., 1996; Crowl and Covich, 1990; Hokit and Blaustein, 1995; Mathis and Hoback, 1997; Smith, 1992; Wilson and Lefcort, 1993; Wudkevich et al., 1997). When prey species detect alarm cues in their surroundings, they immediately show antipredator behaviour including refuge use, dashing, area avoidance, increased shoal cohesion and decreased movement (Chivers and Smith, 1998; Ferrari et al., 2010). The crayfish, *Orconectes virilis*, shows a strong antipredator response involving a reduction in movement when exposed to chemical alarm cues (Hazlett, 1994). Similarly, Wilson and Lefcort, (1993) found that red-legged frog, *Rana aurora*, tadpoles exhibit reduced movement as a result of chemical alarm cue. Moreover, Brown and Smith, (1997) demonstrated that juvenile rainbow trout, *Oncorhynchus mykiss*, show strong antipredator responses to alarm cues by decreasing their time spent swimming, increasing freezing behaviour and taking more time to resume regular feeding behaviour when experiencing alarm cues. Fathead minnows also show increased shoal cohesion and increased shelter use as an indicator of antipredator response in the presence of chemical alarm cues (Mathis and Smith, 1993). These behavioural changes indicate that prey can assess their local predation threats given ambient

noise conditions, but how alarm cue responses are influenced by boat noise has not been reported.

1.3 Research objectives

The objective of my research is to investigate how anthropogenic noise influences the ability of a prey fish to respond to predation risk and how noise influences boldness. I used freshwater prey fish, fathead minnows, as a study species to examine the research questions. In my studies, I looked at the effects of field-based noise and lab-based noise to test the following research questions:

Does the presence of boat noise influence responses to chemical alarm cue?

Prey are known to exhibit antipredator behaviour in the presence of chemical alarm cues and ambient noise conditions. In chapter 2, I examined whether fathead minnows show antipredator behaviour under boat noise conditions. As such, I tested the antipredator responses of minnows when they were exposed to alarm cues in ambient noise or boat noise conditions.

Does the altered noise environment influence boldness in fathead minnows?

Aquatic lab studies are found to produce a significant amount of noise, which is often overlooked by researchers. Such noise may be generated by various sources including a pump, airstone, water filter or other facilities, resulting in different sound pressure levels – all of which are likely to affect fish behaviour. Among these noise sources, some are familiar to fish, and some are not. In chapter 3, I tested the boldness behaviour of fathead minnows in exposure to novel noise environment. As such, I investigated fish boldness through measuring latency to emerge from an isolation chamber as a behavioural assay either in an environment with familiar noise or with novel noise.

Chapter 2: Experiment 1 – Motorboat noise inhibits the alarm reaction of a freshwater fish

This study has been submitted to ‘Animal Cognition’.

Hasan, M.R., Crane, A.L., Ferrari, M.C.O., and Chivers, D.P. (2018). Motorboat noise inhibits the alarm reaction of a freshwater fish.

For the studies included in chapter 2, I undertook the investigations, collected and organized data. Dr. Adam Crane and I analyzed the data and drafted the manuscript. All authors contributed to the final version of the manuscript.

2.1 Abstract

Anthropogenic noise is recognized as a major global stressor of aquatic animals. Such noise pollution can have detrimental effects on hearing sensitivity, communication, navigation, and foraging. However, less is known about the influence of noise pollution on risk perception and antipredator behaviour. Here, we experimentally investigated the effects of motorboat noise on the antipredator behaviour of a freshwater prey fish, the fathead minnow, *Pimephales promelas*. Exposure to motorboat noise caused the total absence of the classical fright reaction of minnows to conspecific alarm cues, whereas an ambient noise control had no such impact. This result supports the 'distracted prey hypothesis' which posits that processing noise distracts prey from processing other information in the brain. In natural habitats, the impairment of antipredator behaviour due to noise pollution potentially has major fitness consequences. How our findings translate to behaviour and ecology and inform management decisions regarding aquatic noise pollution deserves much more scientific attention.

2.2 Introduction

Over recent decades, noise generated by anthropogenic activities has been increasing at an unprecedented rate in aquatic environments due to increased transportation networks (e.g., motorboat traffic), energy exploration (e.g., seismic surveys), construction (e.g., pile driving), fishing, and recreational activities (Graham and Cooke, 2008b; Hildebrand, 2009; McDonald et al., 2006; Normandeau Associates, 2012; Shannon et al., 2016; Whitfield and Becker, 2014). The problem is exacerbated by the fact that underwater sound travel much farther than sound in the air due to the higher density of water (Cox et al., 2016; Slabbekoorn et al., 2010), and consequently, noise pollution likely has greater impact underwater (Cox et al., 2016). The ecology of aquatic animals is impacted when noise interference overlaps with their sensitive hearing ranges. Examples include detrimental effects on communication, foraging, movement patterns, reproductive success, and survival (Bracciali et al., 2012; Codarin et al., 2009; Nedelec et al., 2014; Normandeau Associates, 2012; Popper and Fay, 2011; Shannon et al., 2016; Simpson et al., 2016b; Slabbekoorn et al., 2010). Motorboat noise, in particular, is known to cause uncoordinated swimming and weakened schooling in tuna, *Thunnus thynnus* (Sarà et al.,

2007), decreased reproductive behaviour in cichlids, *Neolamprologus pulcher* (Bruintjes and Radford, 2013), poor habitat settlement in larval reef fishes, *Pomacentrus nagasakiensis* and *P. amboinensis* (Simpson et al., 2016a), and decreased territory defence in gobies, *Gobius cruentatus* (Sebastianutto et al., 2011).

Predator avoidance is another fundamental aspect of behavioural ecology that has received attention in the context of motorboat noise pollution. The ability to assess local predation risk and respond correctly is critical for the survival of prey species (Lima and Dill, 1990). Some species manage predation risk by changing their morphology or altering the timing of life-history transitions (Relyea, 2002; Riessen, 1999), whereas behavioural defences are more widespread, being rapidly enacted in response to acute threats, and fine-tuned to match the level of perceived threat (i.e., threat-sensitive responses) (Helfman, 1989). However, a few studies have documented altered antipredator behaviour in the presence of motorboat noise (hereafter, boat noise). Eels, *Anguilla anguilla*, and damselfish, *Pomacentrus amboinensis*, are known to exhibit flawed escape responses to predator visual stimuli (Simpson et al., 2016b, 2015), resulting in increased predation-related mortality (Simpson et al., 2016b). Another study documented that stickleback, *Gasterosteus aculeatus*, reacted more quickly to a predator visual stimulus, suggesting increased alertness under boat noise conditions (Voellmy et al., 2014b). However, minnows, *Phoxinus phoxinus*, showed no change in reaction time to the visual threat, revealing interspecific differences in the influence of boat noise (Voellmy et al., 2014b). In contrast to visual stimuli and predator presence, responses toward risky chemical stimuli have not been tested, and other fundamentally important antipredator behaviours such as changes in overall activity levels and refuge use have received little attention.

Our goal, here, was to explore how boat noise affects the antipredator behaviour of fathead minnows, *Pimephales promelas*, a freshwater species that is widely distributed and abundant in North America. Fathead minnows (hereafter, minnows) are well known for their classic fright reaction to Schreckstoff – a substance contained in their skin that is released upon physical damage from a predator (V. Frisch, 1942, 1938). When minnows detect this substance (commonly referred to as 'alarm cue') in their surroundings, they display distinctive behaviours such as dashing, freezing, and increased refuge use (Smith, 1992). Here, we tested whether boat

noise, compared to ambient noise, influences the responses of minnows to alarm cues. As found in previous studies (e.g., Purser & Radford, 2011; Wisenden et al., 2008), we expected the addition of underwater boat noise to elicit only a weak or negligible fright response in the absence of predation risk. However, we predicted that boat noise acts as a stressor that would interfere with the normal fright reaction of minnows to alarm cues.

2.3 Methods

2.3.1 Minnow collection and maintenance

Approximately 200 minnows (unsexed; total length: 20-40 mm) were collected from Pike Lake in central Saskatchewan in July 2017. Minnows were transported to our laboratory and housed in a ~2000 L flow-through tank filled with filtered municipal water (hereafter, water) and maintained at 19°C under a 15:9 h light:dark cycle. The tank contained artificial plant habitat and aeration via a hose with an airstone. Each day, minnows were fed flake food and received a 30% water change.

2.3.2 Alarm cues

We sacrificed four individuals (23–35 mm total length) to make alarm cues. A total of 6.15 cm^2 of skin was removed, homogenized (polytron PT-2500E) in water, and diluted to reach an established concentration of 1 cm^2 of skin per 40 l that is known to elicit a strong fright reaction (Ferrari et al., 2006, 2005; Ferrari and Chivers, 2006). The alarm cue solution was then frozen at -20° C in 100 ml aliquots until being thawed before use.

2.3.3 Noise recordings and playbacks

We recorded ambient and boat noise at five locations within Blackstrap Lake, Saskatchewan, an area that is popular for recreational boating. All recordings occurred from 09:00–13:00 at 3–5 m water depth. At each location, we used an omnidirectional hydrophone (CR1, calibrated sensitivity -198 dB re 1 V/µPa; frequency 0.02–20 kHz; Cetacean Research

Technology, Seattle WA) with a data-acquisition card (SpectraDAQ-200) to record the sound of a boat (Honda 10 metric hp, 5-m aluminum flat bottom John boat with 4-stroke engine) accelerating at various speeds (5–15 km/h) from a distance >10 m. For playback of recordings during experimental trials, we created a single file of ambient noise, and another for boat noise by averaging sound pressure levels using Audacity 2.1.0. The sound spectrums for the playbacks and field recordings were autogenerated in SpectraPLUS (FFT size of 8192 points, Hanning window, 0–3 kHz, Fig. 1). Within the sensitive hearing range of minnows (1–2 kHz, Scholik & Yan, 2002; Fig. 1), boat and ambient noise playbacks were slightly higher than recordings in situ, presumably due to the presence of aeration via an airstone in the tank environment. However, boat noise (93–102 dB) was substantially louder than ambient noise (59–78 dB), and boat noise levels (93–102 dB) closely matched those of previous studies (Simpson et al., 2016b, 2015; Spiga et al., 2017; Voellmy et al., 2014b).

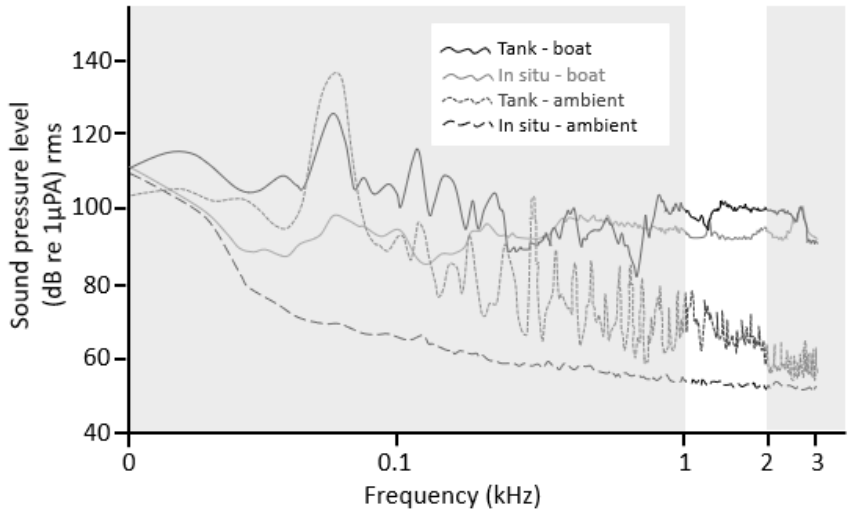

Figure 2.1. Sound pressure levels (dB re 1 µPa) for ambient and boat noise at the field site and from playbacks in laboratory tanks. The unshaded zone between 1–2 kHz represents the sensitive hearing range of minnows (Scholik and Yan, 2002).

2.3.4 Experimental protocol

We used a 2×2 design where minnows were exposed to either distilled water (control) or alarm cues under conditions of either ambient or boat noise. First, minnows were placed individually into 37-l experimental tanks containing gravel substrate, a shelter (a 10×10 cm

ceramic tile with 2-cm PVC legs), and over-head lighting. The front of each tank was covered with a plastic film (5% visual light transmission), allowing us to observe the fish while minimizing visual cues from our presence. Fish were allowed to acclimate to the tank conditions for 24 h before observations were conducted. An upward down facing underwater speaker (ECOXGEAR EcoRox) was placed in the experimental tank. Each trial consisted of three parts: (1) an 8-min pre-stimulus period, (2) the onset of noise paired with a stimulus injection of either 20 ml of alarm cues or water control, and then (3) an 8-min post-stimulus period. Each injection occurred gently through a hose attached to an airstone in the tank, while noise was initiated via a Bluetooth transmitter. The ambient noise treatment consisted of ambient noise playback for the full 8 min, whereas the boat noise exposure consisted of 2 min of boat noise followed by 2 min of ambient noise and then alternated for the remaining time. During both the pre- and post-stimulus periods, we calculated the number of lines that each minnow crossed on a grid (6.3×6.3 cm) and the time spent under shelter. Minnows were tested only once, and sample sizes were 26 per treatment group.

2.3.5 Statistical analysis

For both response variables, we calculated a proportional change [(post-stimulus – pre-stimulus)/pre-stimulus] to account for individual variation in pre-stimulus data. Doing such for time spent under shelter necessitated the conversion to time spent in the open (total trial time – time spent under shelter) to eliminate zero values in the pre-stimulus data. We then analyzed differences in the two proportional responses using a 2-way MANOVA with the chemical cue (alarm cue or water) and the noise treatment (boat or ambient) as fixed factors. Because non-normality and covariance heterogeneity assumptions were not fully met, we used Pillai's trace for its conservativeness (Olson, 1976). In post-hoc analyses (1-way MANOVAs), data were split by noise treatment and the fish responses to alarm cue and water were compared.

2.4 Results

A significant interaction revealed that responses to alarm cues depended on the noise treatment (noise × chemical cue: $F_{2,99} = 8.80$, $P < 0.001$; Fig. 2). In comparison to the control,

fright reactions to alarm cues were strong under ambient noise conditions ($F_{2,49}$ = 19.74, P < 0.001), but these responses were absent in the presence of boat noise ($F_{2,49}$ = 0.07, P = 0.93).

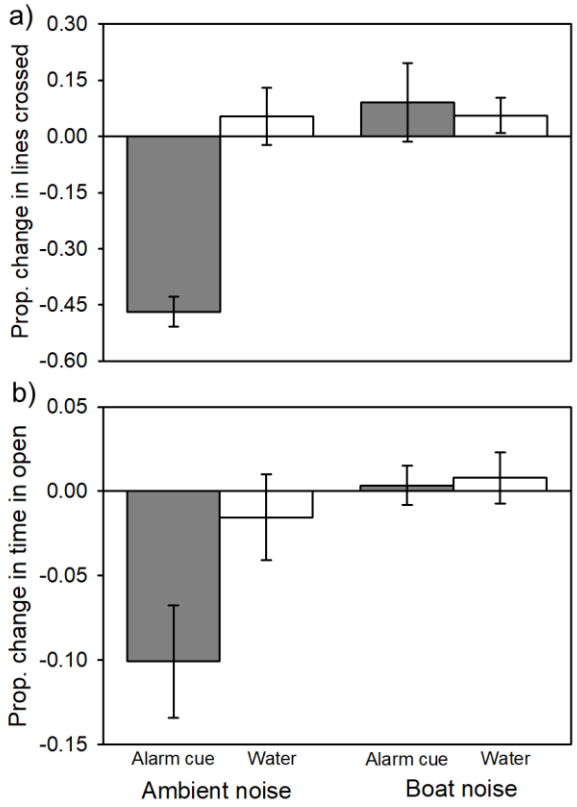

Figure 2.2. Mean (± SE) proportional change in (a) lines crossed and (b) time in open for fathead minnows (*Pimephales promelas*) exposed to distilled water and alarm cue under either ambient or boat noise conditions.

2.5 Discussion

Our results add to the growing body of evidence revealing that exposure to boat noise can interfere with antipredator responses in aquatic systems, documenting for the first time that responses to chemical alarm cues can be impaired. Correctly responding to alarm cues is crucial to many species for predator detection and short-term survival (Lonnstedt et al., 2012; Mirza and Chivers, 2000). Moreover, the probability of longer-term survival can also decrease if predator learning is impaired (Leduc et al., 2004). Whether fish are capable of learning predator recognition under boat noise conditions is a topic of future interest, with an outcome that is likely dependent on the mechanism underlying our results.

We considered the possibility that (1) intense auditory stimuli could physically damage olfactory tissue, but this seems implausible with such a short time frame of noise exposure, and to our knowledge no studies indicate such. Alternatively, increased vigilance under noise conditions might explain the absence of a change in overall activity, but not the absence of a change in shelter use; under our experimental tank conditions, highly vigilant minnows move back and forth rapidly underneath shelter (personal observations). Another potential mechanism is that (2) noise caused an increase in metabolism that promoted energy intake via foraging, as suggested in some studies (Simpson et al., 2016b, 2015; Spiga et al., 2017). Moreover, some studies have documented increased foraging errors due to noise, hence causing increased allocation of time to foraging (Bracciali et al., 2012; Purser and Radford, 2011; Voellmy et al., 2014a). While we did not record foraging behaviour in our experiment, fish did continue to search for food under noise conditions, so we cannot discount this mechanism. However, it again seems unlikely given the acute exposure in our experiment. Alternatively, (3) minnows may have failed to perceive the chemical cues because their attention was redirected toward the source of the sound, a mechanism referred to as the 'distracted prey hypothesis' (Chan et al., 2010). An inability to perceive both auditory and chemical stimuli at once suggests that noise interferes with the processing of chemical information in the fish brain. Fish use a variety of adaptations for detecting acoustic stimuli (e.g., inner ears, lateral line, and swim bladder) that are transferred to the telencephalic lobe in the forebrain (Bass and Lu, 2006; Bass and McKibben, 2003). There, the lateral and medial divisions of the pallium process both auditory and olfactory stimuli (Northcutt, 2006). Thus, interference with processing chemical stimuli likely occurs in this brain region, but to our knowledge the molecular mechanism behind the modulatory effects of noise on sensory processing in fish remains unexplored. However, in rats, *Rattus rattus*, cognitive impairment from elevated noise appeared mediated by disruption of a signaling receptor (glutamate-N-methyl-D-aspartic acid) that alters phosphorylation of a protein (tau) associated with cognitive deficits and neurodegeneration (Cui et al., 2012).

Regardless of the mechanism, our results provide clear evidence that alarm reactions can be inhibited by boat noise. Such noise is likely to have adverse effects on a wide range of aquatic species, but we know little about the severity and longevity of effects (Cox et al., 2016)

or the impact of noise in natural communities (e.g., noise can affect both prey and their predators) (Simpson et al., 2016b). Indeed, community ecology, particularly in the context of fisheries management and conservation, deserves much further attention, with behavioural effects potentially driving large-scale outcomes (Blumstein and Fernández-Juricic, 2010). In some cases, it may be prudent to implement or modify regulations to minimize the impacts of boat noise in biodiversity hotspots or sensitive habitats. Approaches to reducing boat noise may include the implementation of quiet zones, speed restrictions, or the required use of mufflers or low-volume engine models (Haren, 2007; Leaper and Renilson, 2012; Würsig et al., 2000). Future study is needed to understand the need and effectiveness of variation in these approaches to noise management.

Chapter 3: Experiment 2 – Altered acoustic environments influence boldness in minnows

This study has been submitted to ‘Applied Animal Behaviour Science’.

Hasan, M.R., Crane, A.L., Poulin, N.P., Ferrari, M.C.O., and Chivers, D.P. (2018). Altered acoustic environments influence boldness in minnows.

For the studies included in chapter 3, I undertook the investigations, collected and organized data. Dr. Adam Crane and I analyzed the data and drafted the manuscript. All authors contributed to the final version of the manuscript.

3.1 Abstract

Human-induced noise has a pervasive influence on the behaviour of animals in their natural environment, but little scientific attention has gone toward noises that regularly affect animals being maintained in captivity for research purposes. Here, we assessed underwater aquarium noise produced from two types of aeration equipment (an airstone diffuser attached to an air pump vs. aeration from a mounted aquarium filter) and used recordings from a hydrophone to characterize these two noise stimuli. For several months, we maintained fathead minnows, *Pimephales promelas,* in a laboratory environment with aeration and noise from an airstone. Then minnows were moved into tanks with either the familiar airstone noise or novel filter noise for four days. We then measured the latency of minnows to emerge from an isolation chamber as a standard measure of boldness behaviour. Exposure to filter noise resulted in decreased boldness, despite being weaker in sound intensity than the airstone noise, leading us to view the novelty of the sound as being representative of a novel environment with unknown threats for minnows. We then returned minnows to their previous noise environment or the opposite noise environment for an additional four days, finding that minnows reverted to bolder behaviour when returning to the familiar acoustic environment (airstone), whereas no acclimation to the novel noise environment (filter) occurred over the additional four days. We discuss these two sources of laboratory noise and encourage a deeper consideration of the intensity and novelty of the acoustic environment in laboratory studies.

3.2 Introduction

Rapid environmental change has become widespread in the form of habitat loss, habitat fragmentation, pollution, and climate shifts, often resulting in exposure to novel situations for animals (Sih et al., 2011). In many cases, altered habitats may be perceived as new environments that contain unknown risks and resources (Sol et al., 2008, 2005). Animals can be attracted to these novel environments (neophilia), or they may show avoidance (neophobia) (Mettke-Hofmann et al., 2009), both of which are manifested by specific changes in behavioural traits such as vigilance, social grouping, and boldness – a risk-taking personality trait (Sih et al., 2004;

Stamps and Groothuis, 2010). Overall, such responses have been documented in a wide range of taxa, can be short- to long-term, and play a key role in driving ecological and evolutionary outcomes (Crane and Ferrari, 2017; Sih et al., 2004; Smith and Blumstein, 2008; Wilson et al., 1994).

The novelty of an environment may be conveyed through a variety of specific habitat features including new structures (Cowan, 1977), new smells (Mitchell et al. in review), or altered temperatures (Forsatkar et al., 2016) or acoustics (Wisenden et al., 2008). Although behavioural responses to novel habitat structure has been well studied, much less is known about novel acoustic environments (Crane and Ferrari, 2017). One study on cichlids, *Pelvicachromis taeniatus*, documented neophobia in response to a novel vibrational pulse (Meuthen et al., 2016), but this single noise was instantaneous and hence not broadly representative of the acoustics of the environment. Several other aquatic studies have exposed animals to pulses of noise in the form of noise from motorized boats, using behaviours such as willingness to feed and distance from shelter as a proxy for boldness (e.g., Holmes et al., 2017). Most of these studies used wild-caught fish that presumably had experience with boat noise in the natural environment. However, in a study by Purser & Radford (2011), fish and boat recordings were obtained from different sites, and thus the noise may have been novel. In that study, exposure to noise resulted in mild fear behaviour and foraging mistakes for stickleback, *Gasterosteus aculeatus.*

Although there is a growing body of research targeting the impacts of human-induced acoustic changes on animal ecology in the natural environment, little attention has been given to the impacts of laboratory noises on experimental animals. For example, in aquatic laboratories, animals are typically provided oxygen via airstone diffusers which have been observed to produce substantially higher (~10 dB) noise than ambient field conditions (Hasan et al. in review). Other potential sources of noise in aquatic laboratories include air pumps, water pumps, water filters, ventilation, noise from adjacent laboratories, and nearby facility maintenance and construction (Davidson et al., 2007; Jemmott, 2010).

Here, we tested how exposure to an environment with novel acoustics, and a subsequent return to an environment with familiar acoustics, affected boldness in fathead minnows,

Pimephales promelas. First, we assayed the latency to emerge from an isolation chamber as a standard measure of boldness (Beckmann and Biro, 2013) when minnows were exposed to an aquarium environment with either familiar noise from an airstone or novel noise from a filter. Then, half of the minnows were exposed to environmental noise that matched their previous environment, whereas the other individuals experienced the opposite noise conditions. A second emergence test allowed us to assess the consistency of boldness behaviour in the presence of familiar noise, whether minnows were acclimating to the novel acoustics, and whether changes in boldness persisted after a return to the familiar acoustics. Individual differences in boldness are often stable over time (i.e., trait validity) but not necessarily repeatable across contexts (Burns, 2008; Carter et al., 2013; Wilson, 1998). Hence, we predicted that fish would decrease their boldness in the presence of novel acoustics and that such behaviour would be consistent over time when the familiar acoustics were maintained, but not when altered. We also predicted that fish would acclimate to the novel acoustic environment and thus become bolder in subsequent exposures.

3.3 Methods

3.3.1 Fish collection and maintenance

In September 2015, we collected ~200 adult minnows from Feedlot Pond in central Saskatchewan using Gee's wire traps. The minnows were then transported to our laboratory and housed in a ~2000 L flow-through tank filled with filtered dechlorinated municipal water (hereafter, water). The tank contained artificial plant structure and aeration via an airstone (Aquaneering, 3×1×1 cm size) that diffused oxygen from a pump (Hiblow hp 40) and produced sound within the sensitive hearing range of minnows (1–2 kHz; Scholik & Yan, 2002) at 81–95 dB (Fig. 1), as recorded with an omnidirectional hydrophone (CR1, calibrated sensitivity -198 dB re 1 V/µPa; frequency 0.02–20 kHz; Cetacean Research Technology, Seattle WA) and a data-acquisition card (SpectraDAQ-200). Fish were fed flake food and maintained at room temperature under a 15:9 h light:dark cycle.

3.3.2 Background tanks and sound treatments

In February 2017, we tagged minnows via a subcutaneous injection of different coloured dye (non-toxic acrylic paint) for identification. Fish were then moved into 37-l tanks in groups of 10 individuals and given 3 d to recover from the stress of tagging before the experiment began. The tanks contained water, a shelter (a 10×10 cm ceramic tile with 2-cm PVC legs), and gravel substrate. Each day, fish were fed flake food and received a 30% water change. A plastic film (5% visual light transmission) minimized visual cues from the observer. Aeration was provided via an airstone (81–95 dB at 1–2 kHz; Fig. 1) that provided air from a pump (a Hiblow hp 40 supplying 8 tanks).

The experiment began when fish were moved into new 37-l 'background tanks', again containing water, gravel, and a shelter. For aeration, half of the background tanks were equipped with a familiar airstone, whereas the other half of background tanks provided a novel acoustic environment in the form of aeration via the outflow of a re-circulating filter (Aqua Clear 20) mounted to the side of each tank. Filter and airstone noise differed substantially in sound pressure level (52–78 dB and 81–95 dB respectively, at 1–2 kHz, Fig. 1). We ensured that both conditions provided fish with water that was fully saturated with oxygen (>8 ppm).

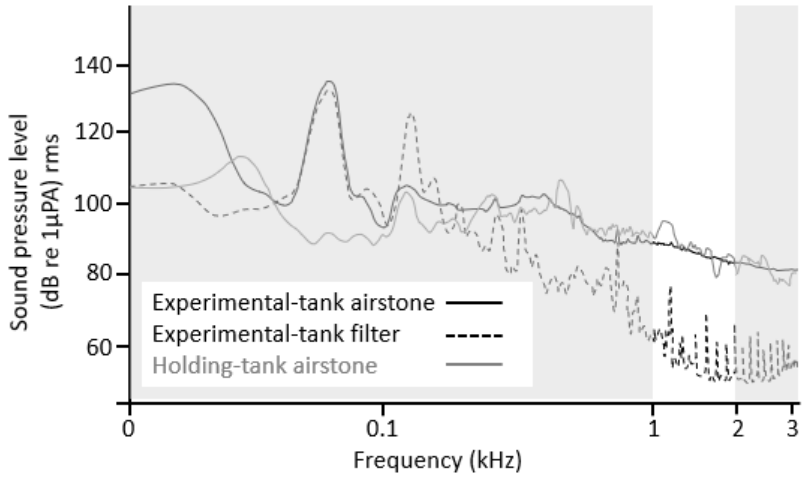

Figure 3.1. Sound pressure levels (dB re 1 µPa) of the holding-tank airstone, the experimental-tank airstone, and the experimental-tank filter at frequency 0–3 kHz. The clear zone (1–2 kHz) represents the sensitive hearing range of minnows (Scholik and Yan, 2002).

3.3.3 Experimental tanks and emergence trials

After 4 days of housing in background tanks with different acoustics, we assessed the boldness of fish using a standard emergence assay (Beckmann and Biro, 2013; Brown and Braithwaite, 2004). First, each minnow was moved individually into a chamber inside a new 37-l tank (Fig. 2). The chamber consisted of a plastic cylinder (9.5 cm diameter, 18.5 cm height) that was inside a slightly larger plastic cylinder (10 cm diameter, 11.5 cm height). Both cylinders were oriented vertically, and the outer cylinder was attached to a plastic base that was anchored by the covering gravel. Both cylinders also had an opening (4.5 cm) that when manually aligned would allow fish to exit the chamber (Fig. 2). A shelter was provided 9 cm in front of the exit to encourage the fish to emerge. We also placed a cover (10×10 cm ceramic tile) over the cylinders to block overhead visual cues. Acoustics in these 'experimental tanks' matched the background conditions (i.e., minnows from background tanks with familiar airstone sound were moved into experimental tanks with familiar airstone sound, and vice versa). Minnows were given 20 min to acclimate to the chamber before opening the exit. We then recorded the latency to emerge when the entire body of the minnow had exited the chamber. If the minnow had not emerged within 20 min, the trial was stopped, and the minnow was assigned a value of 1200 s. We then subtracted latencies from 1200 s to yield an emergence score where higher values represented increased boldness and vice versa.

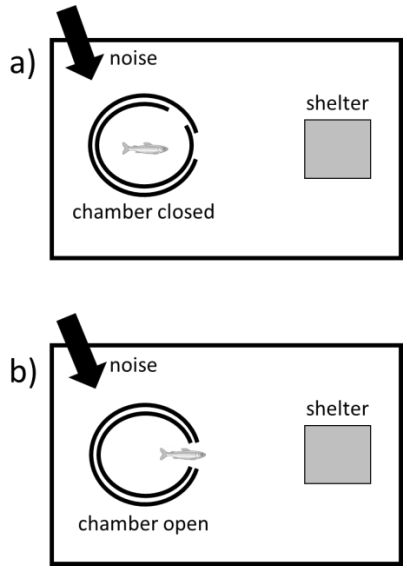

Figure 3.2. Experimental tanks containing an emergence chamber (black circles), a shelter (grey square), and either familiar or novel noise from aeration equipment.

3.3.4 Changes in boldness under matching or altered noise conditions

Following emergence trials, half of the minnows were randomly selected from each treatment were returned to background tanks and given airstone noise for another 4-d period. A second emergence test allowed us to assess the consistency of boldness behaviour in the environment with familiar acoustics (airstone to airstone) and whether changes in boldness would persist with a return to that environment (filter to airstone). The other minnows were returned to background tanks and given filter noise to determine whether minnows were acclimating to the novel acoustics over 8 d (filter to filter) vs. a new exposure to the novel noise as a control (airstone to filter). Hence, the background noise treatment (familiar vs. novel) was crossed with the second (hereafter, current) noise treatment (either the more familiar airstone or the relatively novel filter) in a 2×2 design (Fig. 3).

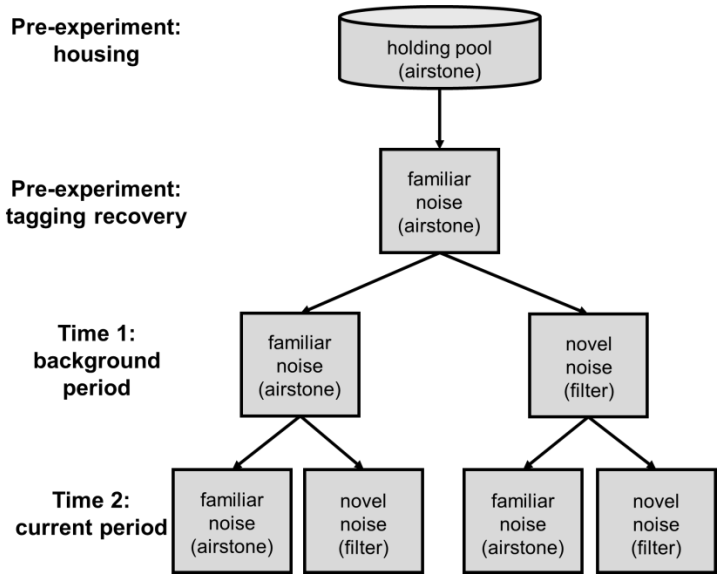

Figure 3.3. Flow chart depicting experimental treatments and phases involving familiar noise from airstones and novel noise from filters.

3.3.5 Statistical analysis

Although our design was well suited for a repeated-measures ANOVA, our data had extremely skewed distributions, which led us to use nonparametric analyses. For data from the first emergence test, we used a Mann-Whitney test to assess differences in boldness between the familiar and novel acoustic treatments. For data from the second emergence test, we used Wilcoxon tests (adjusted for ties) to determine whether boldness was altered in each of the four treatment combinations. We adjusted alpha (α=0.05 to 0.0125) for multiple comparisons with Bonferroni corrections. Sample sizes were 28–30 per group.

3.4 Results

Following the background period, our emergence tests revealed a significant difference between the treatments, where minnows showed decreased boldness in the environment with novel acoustics (U_{117}=817.5, P<0.001; Fig. 4), despite that environment being quieter (~23 dB; Fig. 1). We found no evidence that boldness changed when the familiar acoustics remained consistent (α=0.0125, W_{30}=183, P=0.66), and a return to the familiar environment caused minnows to become bolder (α=0.0125, W_{22}=36, P=0.003). As revealed during the first period, altering the acoustic environment from familiar to novel again led to decreased boldness (α=0.0125, W_{27}=30, P<0.001), and we found no evidence of acclimation to the novel acoustics over an additional 4 d of exposure (α=0.0125, W_{17}=37, P=0.065).

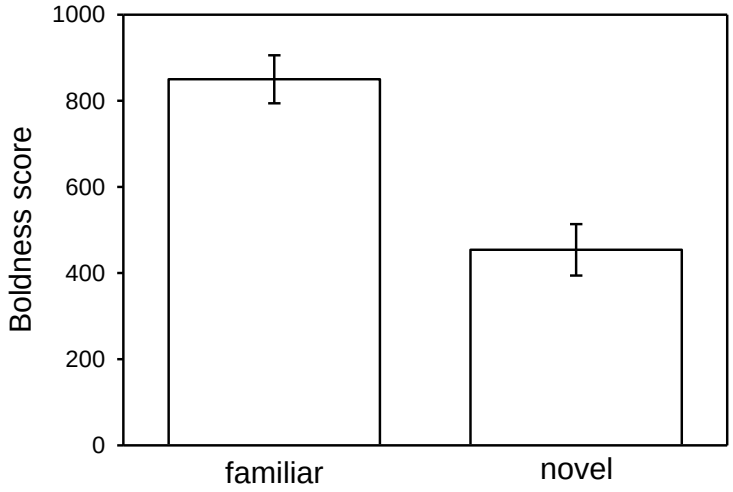

Figure 3.4. Mean (± SE) boldness score (1200 s – latency to emerge) for minnows exposed to familiar airstone noise or novel filter noise.

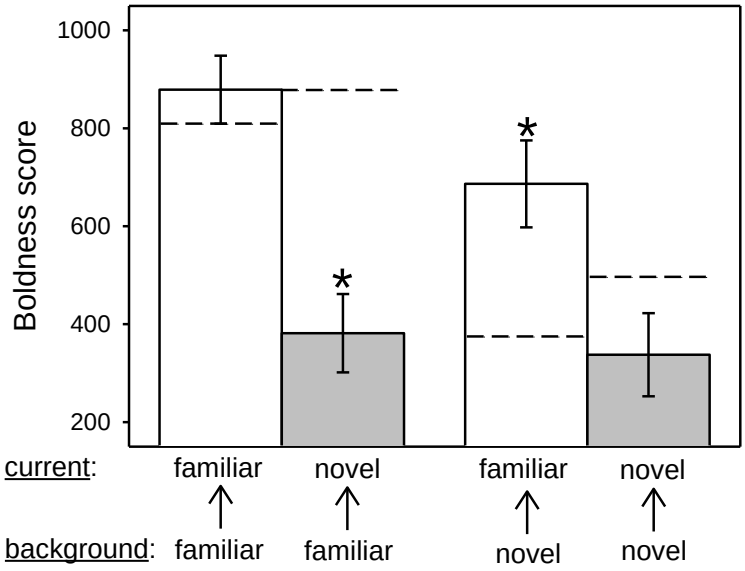

Figure 3.5. Mean (± SE) boldness score (1200 s – latency to emerge) for minnows that were previously exposed to either familiar airstone noise (white bars) or novel filter noise (grey bars) during a background period and then exposed to either the same noise (consistent) or the opposite noise (altered) during a recent period. Asterisks indicate significant changes in boldness between the first (dashed lines) and second exposure.

3.5 Discussion

Novel acoustic environments appear to cause a fearful state in minnows, as indicated by their decreased boldness. Therefore, our findings may be consistent with other studies demonstrating neophobia toward novel sounds (Brocke et al., 2006; Meuthen et al., 2016), and that such a phenotype can be manifested in the same fashion as toward novel structures and smells (e.g., Brown and Jones, 2016; Hartman and Lawler, 2014). The reversal of this phenotype upon returning to the familiar acoustic environment suggests that minnows can recover fairly

quickly from the stress of an environment with novel acoustics. However, when novel acoustics persist, such a phenotype may last for several days, as we found no evidence for acclimation to the novel noise over the 8-d period. In response to novel odours, fearful behaviour can last a few weeks, and potentially longer under higher levels of risk (Brown et al., 2015), but to our knowledge no studies have assessed the longevity of neophobia toward acute or chronic acoustic disturbances.

In the natural environment, animals are increasingly being exposed to novel acoustics resulting from human activities. Many negative affects of such noises have been documented in both terrestrial and aquatic systems. While the impacts of noise exposure are often assessed in laboratory experiments, researchers may have a tendency to overlook routine laboratory noises and not consider the influence of mild and novel sounds. Such noises are a concern (Popper, 2003; Richardson et al., 1998) because they can interfere with normal animal behaviour, potentially impacting experimental results if treatment-noise interactions exist. Noise in aquaria may be dismissed even more regularly than noise in laboratories housing terrestrial organisms because researchers do not hear the intensity of the noise through water. We recommend that researchers carefully consider the sources and impacts of laboratory noise, particularly in the context of determining the intensity of various equipment noises, and recognizing that altering such equipment can cause acoustic novelty that may necessitate long acclimation periods before experimentation should begin.

Although the results of this study are consistent with the hypothesis that the novelty of the sound environment caused decreased boldness in minnows, we did not attempt to determine whether specific sound characteristics (e.g., intensity vs. frequency) may have caused the changes. Clearly the noise from the airstone in our study was louder than the filter noise, and fish have been shown to decrease growth and reproductive behaviour in aquaria with such an increase (Banner and Hyatt, 1973). However, the fish in our study were bolder in the presence of the louder noise (airstone), suggesting that the increased volume was not a factor in their response, although we cannot dismiss the possibility that a quieter environment was frightening to minnows. Because the acoustic stimuli in our study occurred steadily over the 20-min acclimation period and subsequent trial, the speed the sound traveled was likely inconsequential.

Laboratory fishes are important biomedical models for surgical procedures, and genetic and neurobiological studies (Amatruda et al., 2002; Chico et al., 2008; Lieschke and Currie, 2007), as well as for commercial food production (Casebolt et al., 1998). Hence, these aquatic animals deserve substantial welfare attention in the context of laboratory noise stressors, as do their terrestrial counterparts. Future research should consider not only how the behaviour of laboratory animals is influenced by their acoustic environment, but also how stress physiology might be altered, leading to decreased growth and reproductive rates. A more obvious source of confounding variation arose from differences in water flow between the treatments, which was roughly twice as fast in the filter noise treatment, as indicated by *a posteriori* tests with dye. Thus, the possibility that differences in flow rates affected boldness in this study cannot be discounted and deserves future study among aquatic laboratory animals.

Chapter 4: General Discussion

4.1 Noise and predation

Antipredator responses of fathead minnows to chemical alarm cues are well-studied, and the present study shows that such behaviours can be altered in response to anthropogenic noise. In chapter 2, I presented an investigation where I measured antipredator behaviours of fathead minnows in response to alarm cue under the playback of boat noise. I found a weak fright response, no significant change in shelter use or overall activity levels of minnows in the absence of alarm cue under boat noise conditions. Similarly, Purser and Radford, (2011) found only mild fright response, no change in movement or hiding of three-spined sticklebacks, *Gasterosteus aculeatus,* exposed to brief and prolonged boat noise. Interestingly, I found that alarm cues were not able to elicit an antipredator response in fathead minnow upon exposure to boat noise conditions. As I mentioned in chapter 2, this inability may be the result of either (1) a change in foraging decisions stemming from increased metabolic rate in a noisy environment or (2) the modulatory effects of noise on sensory processing in the fish brain.

4.2 Noise and boldness

In chapter 3, I presented the results of my experiment into the effects of novel laboratory acoustics on boldness in fathead minnows. I measured boldness of minnows using emergence trials from an isolation chamber as a behavioural assay. I found that minnows increased their latency time to emerge in response to the presence of novel noise – which indicates a fearful state. Similarly, a fear response was also found in cichlids upon exposure to novel sound (Meuthen et al., 2016). It is important to note that similar fear responses also observed in response to novel structures or smells. Brown and Jones, (2016) found that torresian crows, *Corvus orru,* were more wary of a novel object, following colonization of a novel noisy urban environment than when in the wild environment. Likewise, cascades frog tadpoles, *Rana cascada,e* reduced their activity to a novel risk cue (Hartman and Lawler, 2014). This evidence seems a likely explanation for the observed decrease in boldness in the novel sound treatment. I did not, however, find any evidence for acclimation of minnow to the novel noise exposure over

the 8-d period. Although it was found that fear response in guppies, *Poecilia reticulata,* can last a few weeks after exposure to novel risk cue (Brown et al., 2015), the period of time that sound can alter behaviour is unknown. I found that minnows recovered from the stress of the novel acoustic environment sooner when they were transferred to their familiar noise environment. Therefore, types of sound (e.g., novel or familiar, acute or chronic) should be considered cautiously during lab studies.

4.3 Future directions and concluding thoughts

Anthropogenic noise will be a crucial factor affecting global aquatic ecosystems as it is increasing day after day. Therefore, it is necessary to understand how anthropogenic noise affects aquatic ecosystems in the immediate future. Although I have examined a few potential impacts of such stressor on freshwater fish, there is much more that remains unknown.

In the first experiment, I exposed fish to acute noise of motorboats to test the antipredator behaviour of fathead minnows under controlled laboratory conditions. However, in natural habitats, fishes may experience chronic or repeated exposure to boat noise. Thus, understanding how responses of a given prey species can change over time, and if the reactions are dependent on previous experience (e.g., adaptation or acclimation, sensitization) should deserve further research attention. Besides, it is clear that the acute noise exposure has detrimental effects on the antipredator behaviour of minnows. However, we do not know how fast the affected minnows return to normal conditions or if they can compensate in another way. Such recovery time may have long-term fitness-related consequences on survival and reproductive success. Therefore, future research should concentrate on how long the detrimental effects of boat noise on minnows exist.

In nature, two species which exist in the same habitat may have different susceptibility to the same noise treatment, as a result of difference in hearing ability and physiological stress responses. For instance, two sympatric species, sticklebacks, *G. aculeatus,* and European minnows, *P. phoxinus,* showed differential response to a predator visual stimulus in response to the same noise playbacks (Voellmy et al., 2014a). However, we have limited knowledge about

the reactions of other species. Therefore, future research should consider how reactions of minnows-sympatric species are affected by boat noise. In this way, direct comparisons of species that are to the same noise treatment could be made through utilizing the existing data. Moreover, in a predator-prey system, body size could be an important factor in influencing hearing sensitivities and noise tolerances. For instance, in one study predatory dottyback, *Pseudochromis fuscus* were more successful in capturing prey damselfish, *P. amboinensis* when both were exposed to boat noise simultaneously (Simpson et al., 2016b). Therefore, minnows may be expected to suffer more from boat noise in comparison to their natural predators (e.g., northern pike, *Esox lucius*). Furthermore, it is also clear from the second study that the boldness behaviour of a prey species is affected by chronic noise exposure. However, little is known about the personality of a predatory fish species. Therefore, how a predatory fish can change their personality due to noise stressor should deserve further attention.

In conclusion, both studies highlight how anthropogenic noise in the freshwater environment has the potential to impact fish behaviour. As noise is likely to have adverse effects on a wide range of aquatic species, it is more important to include aquatic noise pollution under management plans and policies. Such an approach could be critical in the context of fisheries management and conservation. In situations where boat noise is shown to have negative impacts on fishes, it may be prudent to implement or modify regulations to minimize those impacts during the breeding season or in biodiversity hot-spots and sensitive habitats. In Saskatchewan, there are no regulations on boat noise, and future work should attempt to understand if any would be warranted. My work addressed a gap in our understanding of the effects of anthropogenic noise on a common freshwater fish. I hope this thesis becomes a baseline reference for future research, to investigate the behavioural ecology of fishes exposed to anthropogenic noise.

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